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Use and Selection of Sleeping Sites by Proboscis Monkeys, *Nasalis larvatus*, along the Kinabatangan River, Sabah, Malaysia

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Key Words

Nasalis larvatus · Sleeping tree characteristics · Surrounding trees · Antipredation strategy · Boat survey · North Borneo

Abstract

The choice of a sleeping site is crucial for primates and may influence their survival. In this study, we investigated several tree characteristics influencing the sleeping site selection by proboscis monkeys *(Nasalis larvatus)* along Kinabatangan River, in Sabah, Malaysia. We identified 81 sleeping trees used by one-male and all-male social groups from November 2011 to January 2012. We recorded 15 variables for each tree. Within sleeping sites, sleeping trees were taller, had a larger trunk, with larger and higher first branches than surrounding trees. The crown contained more mature leaves, ripe and unripe fruits but had vines less often than surrounding trees. In addition, in this study, we also focused on a larger scale, considering sleeping and non-sleeping sites. Multivariate analyses highlighted a combination of 6 variables that revealed the significance of sleeping trees as well as surrounding trees in the selection process. During our boat surveys, we observed that adult females and young individuals stayed higher in the canopy than adult males. This pattern may be driven by their increased vulnerability to predation. Finally, we suggest that the selection of particular sleeping tree features (i.e. tall, high first branch) by proboscis monkeys is mostly influenced by antipredation strategies.

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Introduction

Sleeping site selection is crucial for non-human primates. They spend about half of their lives at sleeping sites [Anderson, 1998], and their choice may affect individual survival [Reichard, 1998; Lutermann et al., 2010; Teichroeb et al., 2012]. Sleeping tree selection may be influenced by several factors, such as predation threat, food proximity, parasite avoidance, avoidance of competitors, thermoregulation, risk of falling, need for comfort and social interactions [Hausfater and Meade, 1982; von Hippel, 1998; Di Bitetti et al., 2000; Li et al., 2006; Phoonjampa et al., 2010; Cheyne et al., 2012; Teichroeb et al., 2012]. These factors vary among primate species and are generally not mutually exclusive [Reichard, 1998; Teichroeb et al., 2012]. They depend on species ecology and may affect individual survival and reproductive success [Cheyne et al., 2012; Teichroeb et al., 2012]. Tree characteristics differ according to the sleeping site function (antipredation, food proximity, stability, etc.). Therefore, primates choose a sleeping site that balances their needs or presents the best trade-off to ensure their survival [Hankerson et al., 2007].

Predator avoidance is the main hypothesis found in the literature on sleeping tree selection by primates [Liu and Zhao, 2004; Teichroeb et al., 2012]. Primates are vulnerable when they sleep, and different strategies have been observed to prevent terrestrial predation at night. They can select sleeping trees in order to: (1) make access more difficult for terrestrial predators, i.e. tall emergent trees [Reichard, 1998; Di Bitetti et al., 2000; Cui et al., 2006], high first branches [Liu and Zhao, 2004; Li et al., 2006; Duarte and Young, 2011], crowns without lianas [Phoonjampa et al., 2010; Barnett et al., 2012; Fei et al., 2012] or location on steep slopes [Liu and Zhao, 2004; Fan and Jiang, 2008]; (2) increase concealment, such as with dense canopy cover [Anderson, 1984; Teichroeb et al., 2012]; (3) get a better view to monitor the ground, i.e. less canopy cover [Hankerson et al., 2007], close to rivers [Bernard et al., 2011; Barnett et al., 2012]; (4) provide good escape routes in case of predator approach by high arboreal connectivity with surrounding trees [Hankerson et al., 2007; Fan and Jiang, 2008; Bernard et al., 2011]; and (5) avoid predator presence (proximity to human settlements [Ramakrishnan and Coss, 2001]). Primates tend to select for the structure and location of the sleeping tree. They may also choose to use multiple sleeping sites and therefore rarely sleep at the same site over consecutive nights to prevent predators from predicting their location [Smith et al., 2007; Phoonjampa et al., 2010; Teichroeb et al., 2012].

Food proximity is another frequent hypothesis to explain sleeping tree selection. Primate groups often sleep in the vicinity of the last or next feeding site, which is recognized as a strategy to reduce their time and energy spent travelling [Chapman et al., 1989; von Hippel, 1998; Day and Elwood, 1999; Pontes et al., 2005; Albert et al., 2011]. Nevertheless, generally primates do not sleep directly in food trees because (1) fruits could be used by predators as an indication of the presence of prey, and (2) nocturnal frugivores might seek fruiting trees and disturb sleeping primates [Sugardjito, 1983].

Proboscis monkeys *(Nasalis larvatus)* are endemic to the island of Borneo. They are large, arboreal and sexually dimorphic colobine primates [Bennett and Sebastian, 1988]. As other Asian colobines, they form stable one-male social groups – consisting of a single adult male, several females and their offspring – and all-male groups – composed of males of different ages [Yeager, 1990; Murai, 2006]. Proboscis monkeys are

restricted to coastal mangrove, swamp and riverine forests [Meijaard and Nijman, 2000; Sha et al., 2008; Stark et al., 2012]. They generally forage inland and return to the riverbank in late afternoon to rest and spend the night along the river's edge [Matsuda et al., 2011]. The proximity to the river has been suggested to be an antipredation strategy allowing primates to reduce their attention at sleeping sites – predators, e.g. Sunda clouded leopards *(Neofelis diardi)*, approaching only from the landward side. However, estuarine crocodiles *(Crocodylus porosus)* may also predate on proboscis monkeys when they cross the river [Matsuda et al., 2008b]. Therefore, proboscis monkeys seem to frequently choose sleeping locations where the tributary is narrower or the branch-to-bank distance is shorter, providing them better escape routes by swimming or jumping to the opposite side in case of a predator attack [Matsuda et al., 2008a].

In this paper, we analyse sleeping site selection by proboscis monkey groups along the Kinabatangan River and study how different age-sex classes use different tree heights. Previous studies did not examine the 'food proximity' hypothesis in the sleeping site selection of proboscis monkeys. Here, due to our study design (groups were observed only at sleeping sites and not followed the entire day), we could not test this hypothesis in detail. However, we decided to consider if leaf, fruit and flower – potential food – abundances in the trees at sleeping sites could be determining factors influencing proboscis monkey's choice. Further, we will refer to this as the 'potential food abundance' hypothesis. Moreover, previous studies have documented sleeping tree preferences in proboscis monkeys by focusing on the species and physical characteristics of sleeping trees and comparing them to other available trees in the study area [Matsuda et al., 2008a; Bernard et al., 2011; Feilen and Marshall, 2014]. However, a sleeping tree may not be selected based on only its own physical features, but also on those of the trees surrounding it [Hankerson et al., 2007]. Therefore, to test both the 'antipredation' and 'potential food abundance' hypotheses, we worked at two different scales: fine (sleeping tree) and large (sleeping site) scales. First, we compared sleeping trees to surrounding trees to highlight sleeping tree characteristics in comparison to other available trees located in direct proximity to sleeping trees. Second, we compared sleeping sites to 'non-sleeping' sites (areas along the riverbank where proboscis monkey groups were never observed to sleep throughout the study). At this larger study scale, we aimed to determine the importance of the entire sleeping site.

In accordance to the 'antipredation' hypothesis, we expected that: (1) selected sleeping trees would differ from surrounding (non-sleeping) trees by providing proboscis monkeys better structural traits against predators at night (i.e. tall trees, high first branch); (2) sleeping sites would differ from non-sleeping sites, by offering groups better structural features to reduce night predation risks (i.e. more canopy connectivity and density); (3) sleeping tree characteristics selected for would vary in relation to the social composition of the proboscis monkey group (one-male or all-male), expecting more antipredation features in one-male group sleeping trees as this social group contains more young individuals which are most vulnerable to predation; and (4) as a response to the predation pressure at night, individuals from different age-sex classes would use sleeping trees differently – with vulnerable juveniles and females using higher locations in the sleeping trees. Regarding the 'potential food abundance' hypothesis, we expected that: (5) selected sleeping trees would differ from surrounding trees and (6) sleeping sites would differ from non-sleeping sites, with the former providing proboscis monkeys with a higher abundance of leaves, fruits and flowers.

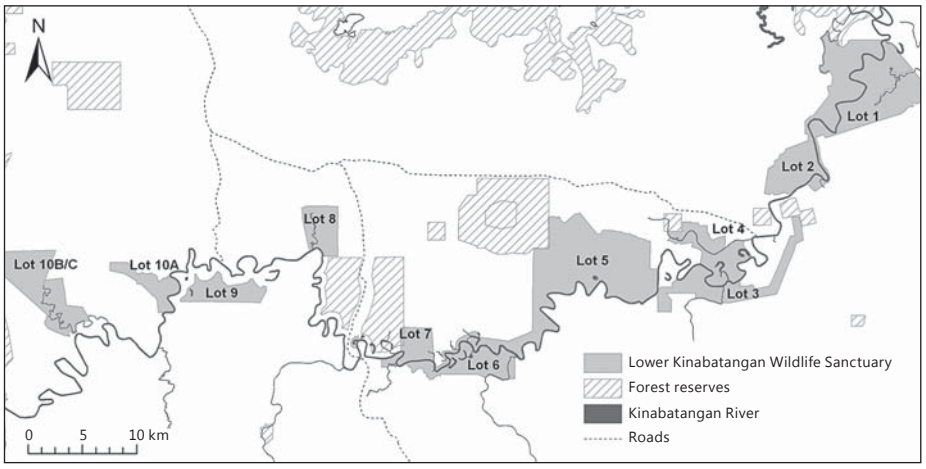

Fig. 1. Map of the Lower Kinabatangan Wildlife Sanctuary with the 10 forest blocks/lots along the Kinabatangan River.

Materials and Methods

Study Site

We conducted our study from November 2011 to January 2012 in riverine forests along the Kinabatangan River, in the Malaysian State of Sabah. The Kinabatangan River is the largest river in Sabah, flowing from 560 km inland to the east coast and the Sulu Sea. In our survey area, the river is approximately 100 m wide. The major habitat types of the Kinabatangan flood plain are lowland dry forest, seasonally flooded forest and mangrove forest [Abram et al., 2014]. Our study took place inside lots 5 and 7 of the Lower Kinabatangan Wildlife Sanctuary (fig. 1). The topography of the study area is mostly flat with low altitudes (under 30 m a.s.l.; Google Earth, 2015).

During our study, we measured daily temperatures, rainfall and river water level at the research station. Monthly rainfall and the mean river level varied from 386.5 mm and 3.19 m (±SD = 0.9) in November 2011 to 535.8 mm and 4.98 m (±SD = 1.3) in January 2012, respectively. Mean monthly minimum and maximum temperatures were constant throughout the study, reaching 24.5 (±SD = 0.8) and 32.5 (±SD = 3.1) °C. At the beginning of the study, sunrise and sunset took place at 05.54 and 17.47 h, and at the study end at 06.25 and 18.16 h (see Sandakan http://www.sunrise-and-sunset.com/).

Data Collection

Use of Sleeping Trees by Individuals

Proboscis monkeys are known to forage inside the forest during the day and come back along water bodies to sleep at night [Matsuda et al., 2011]. This pattern allows researchers to conduct boat surveys before dusk and find groups at their sleeping sites. Therefore, we travelled along the Kinabatangan River every late afternoon in a section between the Danau Girang Field Centre (5°24′48.23″ N, 118°2′17.94″ E) to a point located 6.5 km upstream. We focused our observations on the north riverbank and randomly selected one of the proboscis monkey groups present on the river edge. We (V. Thiry) conducted behavioural observations from 17.00 h – the time of day when groups start to settle at their sleeping site locations – until 18.00–18.15 h. We used the instantaneous scan-sampling method [Altmann, 1974], with a 15-min interval. During each scan, the observer recorded the age-sex class of each individual, its behavioural activity (resting, feeding, moving, other [Matsuda et al., 2009]) and its height in tree (0–10 m; 11–20 m; 21–30 m;

>30 m). We distinguished group individuals by using the descriptions of age-sex classes made by Bennett and Sebastian [1988]. Moreover, we differentiated adult females that were alone from those carrying an infant. Because we did not have the opportunity to follow groups during the day, we were not able, even over consecutive days of observation, to identify individuals and differentiate groups from each other. Therefore, we only considered the group organization and distinguished two types of social composition: 'one-male' groups and 'all-male' groups.

We recorded the sleeping site location with a hand-held GPS unit (Garmin GPS 60CSx). Every morning, we revisited the sleeping site of the previous night to conduct further behavioural observations on the same group (from 06.00 to 07.00 h). After individuals had left the river edge to move inland, we characterized the sleeping habitat, using the plot-sampling method [Ganzhorn, 2003]. To delineate the plots (20 × 20 m), we positioned the sleeping tree in the centre and orientated plots in the same cardinal directions (by using a compass). When a group used several sleeping trees, we defined a point at a mean distance between them as the centre of the plot. When a sleeping tree was selected less than 10 m from the riverbank, we considered the river as the edge of the plot. In each plot, we surveyed every tree with a circumference at breast height (CBH) ≥30 cm.

Terminology

Terms were defined as follows:

1 *Sleeping tree:* a tree in which proboscis monkeys spend the night.
2 *Sleeping site:* an area (plot of 400 m^2) along the river where proboscis monkeys stay overnight; a sleeping site consists of one or several sleeping tree(s) in its centre and surrounding trees.
3 *Surrounding tree:* a tree located in a sleeping site but in which proboscis monkeys do not sleep.
4 *Non-sleeping site:* a randomly chosen area (plot of 400 m^2) along the river where proboscis monkeys were never observed to sleep during the study; a non-sleeping site contains only control trees.
5 *Control tree:* a tree located in non-sleeping sites.

Sleeping Tree Species: Selection or Avoidance

We aimed to test whether the tree species was an important criterion in the selection of night sleeping trees by proboscis monkeys. We calculated the species selectivity (S_i) by comparing the proportion of use (U_i) of each species with the availability (A_i) of trees in (sleeping and non-sleeping) sites along the riverside. We used the following formula:

$$S_i = U_i/A_i$$

where U_i is the number of sleeping trees of species i divided by the total number of sleeping trees, and A_i is the number of trees of species i in plots divided by the total number of trees in plots. We considered that S_i scores >1 indicate a positive selection of the species i in the sleeping choice and S_i scores <1 indicate an avoidance of this species [Feilen and Marshall, 2014].

Sleeping Site Characteristics

In each sleeping site, we distinguished two types of trees: sleeping trees and surrounding trees. We identified each tree – sleeping and surrounding – to the species level and recorded 15 different variables (table 1).

Non-Sleeping Site Characteristics

We could determine different 'non-sleeping sites' along the riverside where proboscis monkeys never slept during the study. We randomly chose 12 plots to characterize the habitats by a grid created on the Software Geospatial Modeling Environment ArcGis 9.3. We only studied trees located ≤50 m away from the riverbank, as a previous study showed that proboscis monkeys generally do not sleep further inland [Bernard et al., 2011]. In these 'non-sleeping plots', we identified each tree (CBH ≥30 cm) to the species level, measured the same 15 variables and used the same methods as those described for sleeping sites.

Table 1. Variables (physical structure and potential food abundance) measured for each tree

Variables	Descriptions	Methods of measurement
CBH	Circumference (cm) at breast height of the tree trunk	Measuring tape
1BGIRTH	Categories of the first branch girth	Estimated by eye. Scale of 1–5: 1 = 0–30 cm; 2 = 31–60 cm; 3 = 61–90 cm; 4 = 91–120 cm; 5 = 121–150 cm
TH	Tree height (m)	Clinometer
1BH	Height (m) of the first branch	Clinometer
CTY	Arboreal crown connectivity with other trees	Estimated by eye. Scale of 0–4, with 0 = the tree is completely isolated, 1 = 25% of the crown edges overlap surrounding trees, 2 = 50%, 3 = 75%, and 4 = the crown edges completely overlap with surrounding trees
DSTY	Tree crown density	Estimated by eye. Scale of 0–4, with 0 = a tree without leaves, 1 = a tree with 75% of sky visibility throughout the crown, 2 = 50%, 3 = 25%, and 4 = a tree in which it is difficult to see the sky throughout the crown
RDIST	Distance (m) from riverbank	Long measuring tool
YOUNGL	Young leaf abundance	Scale 0–4 for the relative abundance of the item visible in the crown, where 0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 >75%
MATL	Mature leaf abundance	
SENEL	Senescent leaf abundance	
BUDS	Bud abundance	
FLOWERS	Flower abundance	
MATFRU	Mature fruit abundance	
UNFRU	Unripe fruit abundance	
VINES	Vine absence or presence	0 indicates absence and 1 presence

Data Analysis

We used the non-parametric Mann-Whitney Wilcoxon test to analyse the comparisons for physical structure and food abundance variables between sleeping, surrounding and control trees. To carry out these tests, we used the R Statistical Software version 3.1.2 (2014). χ^2 tests were computed on Excel version 14.0.0 (2010) to compare binary variables (e.g. absence/presence of vines in canopy) and to identify different proportions. We also conducted discriminant analysis and logistic regression to examine the main features distinguishing sleeping sites used by one-male groups from non-sleeping sites. For this, we used SPSS version 19 (2011). We always used a statistical significance of $p < 0.05$.

Results

Use of Sleeping Trees by Groups

During the study, we conducted 36 morning and 47 afternoon surveys. We conducted 1,333 observations at sleeping sites – 453 in the morning and 880 in the afternoon. The number of occurrences for each kind of social group we observed is 32 one-male (mean ± SD = 13 ± 4 individuals) and 5 all-male groups (mean ± SD = 10 ± 2 individuals). Generally individuals within a group did not sleep together in a single sleeping tree but tended to use an average of 3 (ranging from 1 to 8) sleeping

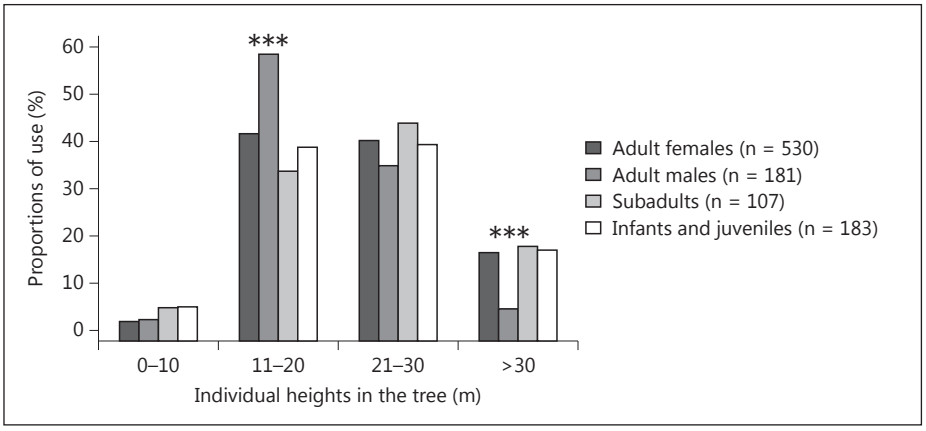

Fig. 2. Use of different heights in the same tree by proboscis monkey individuals of different age-sex classes at sleeping sites along the Kinabatangan River. Adult females refer to adult females with and without infants, and subadults refer to both sexes. *** $p < 0.001$.

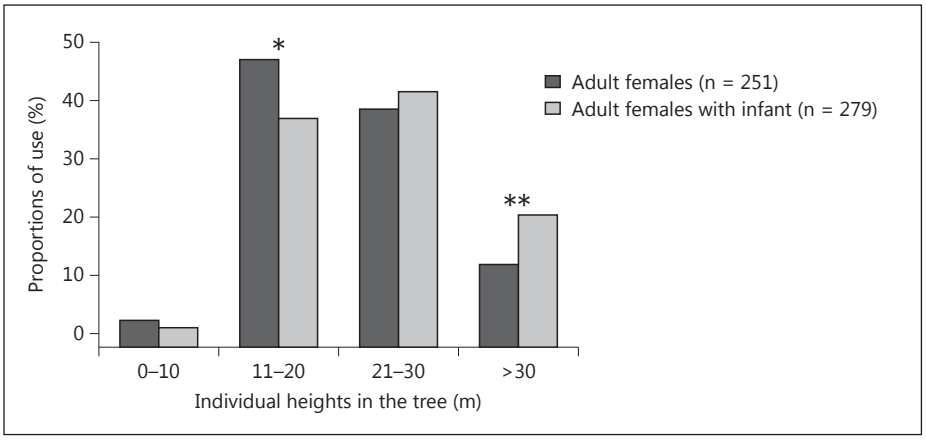

Fig. 3. Use of different heights in the same tree by adult female proboscis monkeys with or without infants at sleeping sites along the Kinabatangan River. * $p < 0.05$, ** $p < 0.01$.

trees. Individuals positioned themselves at different heights in a tree according to their age-sex class ($\chi^2 = 37.39$; n = 1,001; d.f. = 9; $p < 0.001$) (fig. 2). Adult males stayed more frequently at lower heights (between 11 and 20 m high) than other individuals ($\chi^2 = 20.81$; n = 1,001; d.f. = 1; $p < 0.001$) and used the top of the tree canopy (above 30 m) less frequently than others ($\chi^2 = 18.07$; n = 1,001; d.f. = 1; $p < 0.001$).

When we distinguished between the two categories of adult females – with or without infant – we observed a difference in tree height used ($\chi^2 = 10.64$; n = 530; d.f. = 3; $p < 0.05$) (fig. 3). Indeed, adult females with infants stayed at higher positions

Table 2. Tree availability in plots, use and selectivity of sleeping trees by species along the Kinabatangan River

Family	Species	Number of times used	Proportion of use, %	Number of trees in plots	Proportion availability, %	Selectivity coefficient
Malvaceae	*Colona serratifolia*	23	28.40	106	22.94	1.24
Malvaceae	*Pterospermum diversifolium*	15	18.52	19	4.11	4.50
Moraceae	*Ficus racemosa*	14	17.28	12	2.60	6.65
Rubiaceae	*Nauclea orientalis*	13	16.05	26	5.63	2.85
Apocinaceae	*Alstonia* spp.	3	3.70	5	1.08	3.42
Anacardiaceae	*Dracontomelon dao*	3	3.70	8	1.73	2.14
Malvaceae	*Pterospermum elongatum*	2	2.47	22	4.76	0.52
Verbenaceae	*Vitex pinnata*	2	2.47	12	2.60	0.95
Hypericaceae	*Cratoxylum cochinchinense*	1	1.23	3	0.65	1.90
Leguminosae	*Dialium indum*	1	1.23	0	0.00	0.00
Moraceae	*Ficus benjamina*	1	1.23	1	0.22	5.70
Malvaceae	*Kleinhovia hospita*	1	1.23	79	17.10	0.07
Tetramelaceae	*Octomeles sumatrana*	1	1.23	0	0.00	0.00
Unknown	Unknown	1	1.23	17	3.68	0.34

Table 3. Comparisons of physical structure and potential food abundance between *Ficus* sleeping trees (ST) and *Ficus* non-sleeping trees (T and cT) along the north riverbank of the Kinabatangan River

Variables	*Ficus* ST (n = 15)	*Ficus* T and cT (n = 13)	Statistical significance	
CBH, cm	296.79±144.15	127.77±67.42	W = 171	***
1BGIRTH	3.07±1.28	2±1.13 (n = 12)	W = 132	*
TH, m	34.14±13.30	22.47±8.48	W = 149	*
1BH, m	12.76±5.07	10.79±5.92 (n = 12)	W = 99	n.s.
CTY	2.67±0.99	1±0.61	W = 181	***
DSTY	1.57±0.56	1.27±0.60	W = 128.5	n.s.
RDIST, m	15.59±10.67	32.65±19.16	W = 50.5	*
YOUNGL	0.3±0.1	0.25±0 (n = 12)	W = 108	n.s.
MATL	2.2±0.73	1.88±0.06 (n = 12)	W = 116.5	n.s.
SENEL	0.25±0	0.25±0 (n = 12)	W = 90	–
BUDS	0±0	0±0 (n = 12)	W = 90	–
FLOWERS	0±0	0±0 (n = 12)	W = 90	–
MATFRU	0.22±0.27	0.02±0.07 (n = 12)	W = 137.5	**
UNFRU	0.33±0.49	0.15±0.17 (n = 12)	W = 115	n.s.
VINES			χ^2 = 1.1966, d.f. = 1	n.s.
Yes (n = 1)	0 (0%)	1 (100%)		
No (n = 27)	15 (56%)	12 (44%)		

T = Surrounding tree; cT = control tree. Data are means ± SD (even for ranked variables, except for VINES). Wilcoxon test (W) except for the VINES variable (χ^2 test). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, n.s. = non-significant, i.e. $p \geq 0.05$. See the variable descriptions in table 1. The percentages are the relative risks of having vines in tree crown.

Table 4. Comparisons of physical structure and potential food abundance between proboscis monkey sleeping trees (ST) and surrounding trees (T), along the north riverbank of the Kinabatangan River

Variables	ST (n = 81)	T (n = 303)	Statistical significance	
CBH, cm	159.32±101.50	72.20±45.86	W = 4,111.5	***
1BGIRTH	2.10±1.18 (n = 74)	1.25±0.55 (n = 285)	W = 5,978	***
TH, m	27.40±9.92	15.53±8.00 (n = 301)	W = 3,938.5	***
1BH, m	11.73±5.06 (n = 76)	7.86±5.10 (n = 281)	W = 5,852	***
CTY	2.10±1.05	1.86±1.06 (n = 301)	W = 10,669.5	n.s.
DSTY	2.18±0.77	2.03±0.87 (n = 301)	W = 11,019	n.s.
RDIST, m	9.57±7.39	16.24±11.79	W = 16,434.5	***
YOUNGL	0.27±0.07 (n = 80)	0.27±0.10 (n = 238)	W = 9,531.5	n.s.
MATL	2.30±0.74 (n = 80)	2.06±0.76 (n = 238)	W = 7,707.5	**
SENEL	0.26±0.07 (n = 80)	0.26±0.04 (n = 238)	W = 9,241.5	n.s.
BUDS	0.04±0.14 (n = 80)	0.06±0.17 (n = 238)	W = 9,932.5	n.s.
FLOWERS	0.10±0.30 (n = 80)	0.03±0.13 (n = 238)	W = 8,791.5	n.s.
MATFRU	0.30±0.47 (n = 80)	0.07±0.19 (n = 238)	W = 5,883.5	***
UNFRU	0.15±0.28 (n = 80)	0.07±0.19 (n = 238)	W = 7,427	***
VINES			χ^2 = 5.5624, d.f. = 1	*
Yes (n = 73)	8 (11%)	65 (89%)		
No (n = 311)	73 (23%)	238 (77%)		

Data are means ± SD (even for ranked variables, except for VINES). Wilcoxon test (W) except for the VINES variable (χ^2 test). * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, n.s. = non-significant, i.e. $p \geq 0.05$. See the variable descriptions in table 1. The percentages are the relative risks of having vines in tree crown.

(above 30 m) more frequently than those without infants ($\chi^2 = 6.92$; n = 530; d.f. = 1; $p < 0.01$). Females without infants more commonly used heights between 11 and 20 m ($\chi^2 = 5.54$; n = 530; d.f. = 1; $p < 0.05$).

Sleeping Tree Species: Selection or Avoidance

We observed 81 sleeping trees (14 species, 10 families) for proboscis monkeys in 26 nights. The 4 major sleeping tree species were *Colona serratifolia*, *Pterospermum diversifolium*, *Ficus racemosa* and *Nauclea orientalis* (table 2). Together they accounted for 80% of the sleeping trees (n = 65). *C. serratifolia* was the most used tree species for sleeping (n = 23). However, this high number does not reflect a process of selection (selectivity coefficient = 1.24) but only corresponds to the high availability of the tree species along the riverside. However, *Kleinhovia hospita* was also highly available on the riverbank but this species was used only once as sleeping tree. Proboscis monkeys therefore seem to avoid this species (selectivity coefficient = 0.07) in their choice of a sleeping tree. *F. racemosa* was the most preferred sleeping tree species (selectivity coefficient = 6.65). *F. benjamina* also seemed to be selected by proboscis monkeys, but as we only recorded 1 sleeping tree belonging to *F. benjamina*, this choice requires further investigations. By comparing the physical characteristics between *Ficus* sleeping trees and other available *Ficus* trees (sur-

Table 5. Comparisons of physical structure and potential food abundance between sleeping trees selected by one-male groups (OMG ST) and sleeping trees selected by all-male groups (AMG ST) along the north riverbank of the Kinabatangan River

Variables	OMG ST (n = 44)	AMG ST (n = 9)	Statistical significance	
CBH, cm	156.43±115.58	126.44±45.10	W = 223.5	n.s.
1BGIRTH	2.25±1.26 (n = 40)	2.00±0.87	W = 190.5	n.s.
TH, m	27.91±11.98	27.31±9.45	W = 201	n.s.
1BH, m	11.88±5.60 (n = 40)	11.39±4.39	W = 184.5	n.s.
CTY	2.06±1.17	1.94±0.73	W = 205.5	n.s.
DSTY	2.30±0.69	1.33±0.56	W = 338.5	***
RDIST	9.55±9.02	8.65±5.47	W = 186	n.s.
YOUNGL	0.27±0.09 (n = 43)	0.25±0.00	W = 211.5	n.s.
MATL	2.24±0.81 (n = 43)	1.94±0.46	W = 253	n.s.
SENEL	0.26±0.07 (n = 43)	0.31±0.11	W = 156	n.s.
BUDS	0.04±0.16 (n = 43)	0.03±0.08	W = 190.5	n.s.
FLOWERS	0.16±0.40 (n = 43)	0.03±0.08	W = 215	n.s.
MATFRU	0.25±0.46 (n = 43)	0.31±0.48	W = 167.5	n.s.
UNFRU	0.12±0.33 (n = 43)	0.17±0.13	W = 121.5	*
VINES			χ^2 = 5.5624, d.f. = 1	n.s.
Yes (n = 8)	8 (100%)	0 (0%)		
No (n = 45)	36 (80%)	9 (20%)		

Data are means ± SD (even for ranked variables, except for VINES). Wilcoxon test (W) except for VINES variable (χ^2 test). * $p < 0.05$, *** $p < 0.001$, n.s. = non-significant, i.e. $p \geq 0.05$. See the variable descriptions in table 1. The percentages are the relative risks of having vines in tree crown.

rounding and control trees together) in the study area, we observed significant differences for 6 variables (table 3). *Ficus* sleeping trees were closer to the riverbank, taller, with a larger trunk and first branch, and had a more connected crown with more ripe fruits.

Sleeping Tree Characteristics

By comparing the 15 variables between sleeping trees and surrounding trees, we identified 9 significant differences (table 4). Sleeping trees had a wider trunk circumference (CBH), and were located closer to the riverbank than surrounding trees. They were taller than surrounding trees and had higher and wider first branches. The abundance of mature leaves, unripe and mature fruits were greater in sleeping trees than in surrounding trees, and fewer sleeping trees had vines in their crown.

During our behavioural observations at sleeping sites, we recorded the social organization of proboscis monkey groups: one-male or all-male groups. By comparing sleeping trees used by one-male (n = 44) and all-male groups (n = 9), we observed that the crown density and the abundance of unripe fruits were the only two features varying between them. The canopy cover was significantly thicker in one-male group sleeping trees while the unripe fruit abundance was lower (table 5).

Table 6. Comparisons of physical structures and potential food abundance between surrounding trees (T) located in proboscis monkey sleeping sites and control trees (cT) located in non-sleeping sites, along the north riverbank of the Kinabatangan River

Variables	T (n = 303)	cT (n = 159)	Statistical significance	
CBH, cm	72.20±45.86	72.87±35.86	W = 22,468.5	n.s.
1BGIRTH	1.25±0.55 (n = 285)	1.33±0.52 (n = 153)	W = 19,879	*
TH, m	15.53±8.00 (n = 301)	15.79±6.38	W = 22,333.5	n.s.
1BH, m	7.86±5.10 (n = 281)	6.79±3.90 (n = 152)	W = 23,609.5	n.s.
CTY	1.86±1.06 (n = 301)	1.92±1.23	W = 23,804.5	n.s.
DSTY	2.03±0.87 (n = 301)	1.98±0.83	W = 24,873	n.s.
RDIST, m	16.24±11.79	24.11±13.92	W = 16,012.5	***
YOUNGL	0.27±0.10 (n = 238)	0.26±0.07	W = 19,163	n.s.
MATL	2.06±0.76 (n = 238)	1.90±0.82	W = 20,771	n.s.
SENEL	0.26±0.04 (n = 238)	0.25±0.03	W = 19,080.5	n.s.
BUDS	0.06±0.17 (n = 238)	0.03±0.11	W = 19,878.5	n.s.
FLOWERS	0.03±0.13 (n = 238)	0.03±0.09	W = 19,166.5	n.s.
MATFRU	0.07±0.19 (n = 238)	0.15±0.27	W = 15,673	***
UNFRU	0.07±0.19 (n = 238)	0.11±0.24	W = 17,722	n.s.
VINES			χ^2 = 3.3012, d.f. = 1	n.s.
Yes (n = 88)	65 (74%)	23 (26%)		
No (n = 374)	238 (64%)	136 (36%)		

Data are means ± SD (even for ranked variables, except for VINES). Wilcoxon test (W) except for the VINES variable (χ^2 test). * $p < 0.05$, *** $p < 0.001$, n.s. = non-significant, i.e. $p \geq 0.05$. See the variable descriptions in table 1. The percentages are the relative risks of having vines in tree crown.

Sleeping Site Characteristics

Bivariate Analyses

We compared the 15 variables between surrounding trees located in sleeping sites and control trees studied in non-sleeping sites (table 6). Surrounding trees were closer to the riverbank, contained fewer mature fruits and had a thinner first branch than control trees.

Multivariate Analyses

At a wider scale, we focused on sleeping sites (including sleeping and surrounding trees) used by one-male groups to establish a model that discriminates them from non-sleeping sites (including control trees). A multivariate analysis compared these two subsets and brought forward the main tree variables distinguishing them. The results obtained through the discriminant analysis are highly significant (χ^2 = 117.73; d.f. = 9; $p < 0.001$). The analysis extracted 9 discriminant variables (CBH, 1BH, CTY, DSTY, RDIST, MATL, BUDS, FLOWERS and MATFRU – see table 7 with the bivariate outcomes), which together allow us to classify a site as sleeping or non-sleeping, with a probability of 78.81%. We did not include VINES because categorical variables are not allowed in discriminant analyses. We then conducted a logistic regression (backward elimination) with VINES and the 9 variables retained by the first analysis. This second model highlighted a combina-

Table 7. Predictors of sleeping sites used by one-male groups resulting from the first discriminant analysis and VINES: bivariate tests (n = 292).

Predictors	ST+T (n = 133)	cT (n = 159)	p
CBH, cm	84.11±71.39	72.87±35.86	0.101
1BH, m	8.35±6.13 (n = 126)	6.79±3.90 (n = 152)	0.014
CTY	1.86±1.06	1.92±1.23	0.006
DSTY	2.21±0.80	1.98±0.83	0.013
RDIST, m	13.02±9.61 (n = 124)	24.11±13.92	<0.001
MATL	2.08±0.80 (n = 124)	1.90±0.81	0.055
BUDS	0.07±0.21 (n = 124)	0.03±0.11	0.031
FLOWERS	0.08±0.27 (n = 124)	0.03±0.09	0.019
MATFRU	0.06±0.16 (n = 124)	0.15±0.27	<0.001
VINES			0.344
Yes (n = 48)	25 (52%)	23 (48%)	
No (n = 244)	108 (44%)	136 (56%)	

ST = Sleeping trees; T = surrounding trees; cT = control trees. p values assessed by t test except for VINES (Fisher's exact test). The percentages are the relative risks of having vines in tree crown.

tion of 6 significant variables (CBH, 1BH, CTY, RDIST, BUDS, MATFRU) contributing to a good prediction (76.2%) of both sites ($\chi^2 = 116.91$; d.f. = 6; $p < 0.001$) (table 8).

Discussion

In this study, we found that proboscis monkeys were selecting the physical features of their sleeping tree, as well as the abundance of foliage and fruit in the tree. We showed that surrounding trees also influence their selection of sleeping sites along the riverbank. We suggest that the antipredation strategy is the main factor for explaining proboscis monkey sleeping site use and choice, while the food abundance factor requires further investigations.

Many factors may influence sleeping site selection in primates [Di Bitetti et al., 2000; Phoonjampa et al., 2010; Teichroeb et al., 2012]. Here we investigated the selection of sleeping sites by proboscis monkeys along the Kinabatangan River by studying the species, physical structure and potential food availability of sleeping and surrounding trees. Staying higher in the canopy is an advantage in terms of predator avoidance as this reduces the risk of being attacked by a terrestrial animal [van Schaik et al., 1983; Anderson, 1984; Reichard, 1998]. We recorded significant differences between age-sex categories in the way proboscis monkey group members occupy different heights within a sleeping tree. The more vulnerable individuals, such as infants and juveniles, slept higher in the canopy than adult males. We also observed that adult females with infants often occupied higher places than adult females that were alone. This was, presumably, because the higher sites provided better protection from predators for the infants. These patterns of sleeping tree use have also been observed in

Table 8. Predictors of sleeping sites used by one-male groups (n = 269 after exclusion of missing values)

Predictors	Coefficient	Odds ratio	CI	p
CBH	0.009	1.009	1.001 – 1.017	0.012
1BH	0.103	1.108	1.025 – 1.199	0.010
CTY	–0.440	0.644	0.473 – 0.878	0.005
RDIST	–0.111	0.895	0.867 – 0.923	<0.001
BUDS	3.316	27.539	3.079 – 246.78	0.003
MATFRU	–4.629	0.010	0.001 – 0.071	<0.001
Intercept	1.297	3.659		0.005

Logistic regression model with a backward stepwise selection of the predictors. In this model we used VINES and the 9 predictors selected by the previous discriminant analysis (level of significance ≤ 0.1). DSTY, MATL, FLOWERS and VINES are excluded from the initial list because they were not statistically significant. CI = 95% confidence interval.

other species, such as the Sumatran and Bornean orang-utans *(Pongo abelii* and *P. pygmaeus)* [Sugardjito, 1983; Setiawan et al., 1996] and the lar gibbon *(Hylobates lar)* [Reichard, 1998].

Proboscis monkeys are known to return to spend the night along the riverbank. Higher food availability and lower air temperatures in riverine habitats are unconvincing factors to explain this river refuging, as these features are not strongly different from inland habitats [Matsuda et al., 2011]. It is more generally considered to be an antipredation strategy. By selecting a tree at the riverside, individuals have to guard only the landward side, which reduces the risks of surprise predator attacks [Matsuda et al., 2008b]. When the river water level was high at our study site (after several rainy days), we could not find proboscis monkey groups sleeping along the edge of the river. We suggest that flooded forest grounds provide proboscis monkeys with the required protection against terrestrial predators, so that they did not need to travel to the riverbank to find sleeping site refuges [Matsuda et al., 2010].

While the proximity to the river was a determining factor in sleeping site choice, we also emphasized the importance of some physical characteristics of trees. For example, groups preferentially chose tall and large-trunked sleeping trees. These characteristics correspond to proboscis monkeys' choice at other study sites [Bernard et al., 2011; Feilen and Marshall, 2014]. We found sleeping trees had wider first branches, as did Bernard et al. [2011]. Large trees and wide branches may provide comfort and security to individuals, allowing them a better position and reducing the risks of falling, especially when faced with strong winds or wet weather [Di Bitetti et al., 2000; Bernard et al., 2011]. The strong sexual dimorphism in proboscis monkeys, with adult males (20 kg) weighing twice as much as females (10 kg) [Bennett and Sebastian, 1988; Yeager, 1990], could explain their pattern of sleeping tree use – an adult male requiring larger, and most often lower, branches to support its weight. Social relations might also be improved in large sleeping trees, by allowing several or all group members to stay together [Di Bitetti et al., 2000; Bernard et al., 2011]. Feilen and Marshall

[2014] suggested proboscis monkeys might choose tall emergent sleeping trees to reduce mosquito disturbance and therefore minimize the risk of disease. The selection of tall trees also means that the primates are safer as they can sleep further away from terrestrial predators [Cheyne et al., 2012]. We found groups selected trees with first branches higher than surrounding trees and less often with vines in their crown. Both features also support the 'antipredation' hypothesis. Indeed, vines could hide snakes – potentially predating on proboscis monkey infants or juveniles [Matsuda et al., 2008b] – while choosing trees with a higher first branch may reduce the accessibility by terrestrial predators [Day and Elwood, 1999; Liu and Zhao, 2004; Li et al., 2006; Duarte and Young, 2011].

Overall, we did not find that sleeping trees had a denser canopy cover than other trees in the forest, which is similar to the findings of Bernard et al. [2011] and Feilen and Marshall [2014]. However, by focusing on the social organization of the group, we observed that leaf coverage might influence their choice of sleeping trees. Indeed, the crown foliage was denser in sleeping trees used by one-male groups than in those used by all-male groups. This selection might reflect an antipredation strategy because a thicker canopy could better hide more vulnerable individuals from terrestrial predators [Teichroeb et al., 2012]. This choice seems particularly relevant for one-male groups as they include more vulnerable individuals, such as juveniles and infants. In all-male groups, where several adult males are able to protect other group members, a dense canopy might play a less significant role in predation avoidance. The selection of different trees for sleeping and feeding is another antipredation strategy. Fruits could also be used by predators as an indication of the presence of prey [Sugardjito, 1983]. We suggest that one-male groups may follow this strategy by choosing sleeping trees with less unripe fruits than those chosen by all-male groups. Nevertheless, further studies should test such hypotheses as our sampling effort for sleeping trees used by all-male groups was small (n = 9). Finally, connectivity between trees appears to be a controversial factor between study sites. While proboscis monkeys along the Garama River (Sabah, Malaysia) preferred connecting trees [Bernard et al., 2011], they tended to select emergent sleeping trees without connections to surrounding trees at Tolak River (West Kalimantan, Indonesia) [Feilen and Marshall, 2014]. In our study, bivariate comparisons show that connectivity is not an influencing factor that distinguishes sleeping trees from surrounding trees. However, multivariate analyses suggest this feature is crucial when considering the site in its entirety.

We expected sleeping sites would include trees with some antipredator characteristics such as better crown connectivity, denser foliage cover or higher first branches. However, we found surrounding trees and control trees were relatively similar to each other, with the exception of the following 3 variables: surrounding trees were closer to the riverbank, contained fewer mature fruits and had a thinner first branch. Nevertheless, when we conducted multivariate analyses with sleeping sites used by one-male groups and non-sleeping sites, we obtained interesting results. The models retained several combined variables that distinguished both types of sites (sleeping or non-sleeping). The real interest of this multivariate method was to create a model that might be useful to determine the significance of areas by only assessing few variables (CBH, 1BH, CTY, RDIST, BUDS and MATFRU). The model might potentially reduce the number of measurements researchers would have to collect for characterizing sleeping sites of proboscis monkeys.

We also considered the 'potential food abundance' hypothesis by investigating the abundance of leaves, fruits and flowers in sleeping and surrounding trees. We found that individuals appeared to select sleeping trees with more mature leaves, unripe and ripe fruits than surrounding trees. By referring to a previous study conducted in the Kinabatangan region [Matsuda et al., 2009] as well as to our feeding records at sleeping sites, we noticed that more than 80% of the trees (sleeping, surrounding and control) belonged to species that proboscis monkeys are known to consume. However, it is too early to be sure that food abundance is a significant factor in sleeping site selection, as we considered leaf, fruit and flower abundances for all tree species present in our plots, whether they were consumed or not by proboscis monkeys at that time. Nevertheless, sleeping in trees rich in food items is the opposite of what other species do: the Sumatran orang-utan and the agile gibbon avoid sleeping in feeding trees and prefer to spend the night in close proximity [Sugardjito, 1983; Cheyne et al., 2012]. Future studies should investigate in depth the 'food proximity' hypothesis, by recording the distance between sleeping trees and the last and first feeding trees of the day. It is known that food availability, especially of fruits, influences proboscis monkeys' daily path lengths and activity budget [Matsuda et al., 2009, 2014], and may impact their sleeping choices as well.

Our study shows that the physical structure of sleeping trees is a determining factor in the selection of sleeping sites by proboscis monkeys along the Kinabatangan River. Even if some sleeping tree species seemed to be preferred (e.g. *Ficus* spp.), their individual physical structure appeared to play a significant role in the selection process. These sleeping trees were tall, closer to the river, with a wide trunk and first branch, and had a more connected crown than non-sleeping trees (surrounding and control) from the same species. The multivariate model asserts the importance of the overall area – sleeping trees as well as surrounding trees – in the choice of sleeping sites by proboscis monkeys, a finding that should be considered in management decisions. While the antipredation strategy can explain many sleeping tree features observed in our study area, other factors such as comfort, disease avoidance, social interactions and, especially, food abundance should also be considered in the selection process.

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